
DIVERSIFICATION OF ASCLEPIADOIDEAE (APOCYNACEAE) IN THE NEW WORLD¹

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ABSTRACT

Plastid sequences of *trnL-F* are used to estimate the age of biogeographical events in New World Asclepiadoideae. These data suggest that the subfamily arose somewhere in the Old World in the Late Eocene (40 million years ago (Ma)) and that there were at least four independent episodes of dispersal to the New World. The MOG clade, comprising Metastelmatinae, Oxypetalinae, and Gonolobinae, probably colonized South America through transoceanic dispersal from Africa at 32 Ma. The three subtribes emerged at 24 Ma, radiating 15–16 Ma. *Cynanchum* L. subg. *Mellichampia* (A. Gray) Woodson (Cynanchinae) only arrived in the New World at 24 Ma and has since diversified gradually. *Asclepias* L. (Asclepiadinae) probably arrived in the New World through the Bering Strait at 20 Ma, dispersing to South America before the emergence of the Isthmus of Panama. More recently, tropical *Marsdenia* R. Br. (Marsdenieae) probably arrived in the New World by long-distance dispersal at 16 Ma. Most diversification in New World Asclepiadoideae is estimated to have occurred during the Miocene. The synchrony of events suggests an environmental influence on the diversification of the lineages. Nevertheless, individual rates of diversification point out the importance of intrinsic factors.

Key words: Apocynaceae, Asclepiadoideae, biogeography, molecular dating, Neotropics, phylogeny, systematics.

The Asclepiadoideae comprise ca. 3000 species, around 40% of them in the New World (Meve, 2002). Although the Neotropics is one of the centers of diversity for Asclepiadoideae, little has been done to understand the evolution of this subfamily in the region. Most studies were restricted to traditional taxonomy, and classifications have been pragmatic and artificial (Rapini, 2002). During the turn of the millennium, however, the introduction of cladistic studies, especially those based on molecular phylogenetics, reflected a changing perspective toward the classification of Asclepiadoideae (Rapini et al., 2003, and references therein). Despite this progress, only a few studies (e.g., Goyder, 2006) have explored the biogeography of the subfamily.

The hypothesis of African origin for the Asclepiadoideae has long been assumed, predicted by their high diversity, both in the number of species and higher taxonomic levels in Africa, and confirmed by the phylogeny of the group, which is marked by a basal grade composed of Old World, predominantly African, taxa (Sennblad & Bremer, 1996; Civeyrel et al., 1998; Potgieter & Albert, 2001; Liede, 2001; Rapini et al., 2003). The New World Asclepiadoideae are divided into four lineages (Rapini et al., 2003). The largest one has been denominated MOG and is composed of

Metastelmatinae, Oxypetalinae, and Gonolobinae, plus the recently recognized subtribe Orthosiinae and a basal grade formed by *Pentacyphus* Schltr. and *Diplolepis* R. Br., respectively (Liede-Schumann et al., 2005). Two other New World groups, namely *Cynanchum* L. subg. *Mellichampia* (A. Gray) Woodson (Cynanchinae) and *Asclepias* L. (Asclepiadinae), are nested within the predominantly Old World MOG's sister clade referred to as ACT, which comprises the subtribes Asclepiadinae, Cynanchinae, and Tylophorinae (Rapini et al., 2003). The fourth clade is the New World *Marsdenia* R. Br. (Marsdenieae), the only group bearing erect pollinia; the other three clades belong to the Asclepiadeae and possess pendent pollinia.

Despite references to Apocynaceae (e.g., LaMotte, 1952; Brown, 1962) that include the extant genus *Alyxia* Banks ex R. Br. (Müller, 1981) in the Paleocene, molecular data (Wikström et al., 2001) and the most reliable fossil evidence of their earliest appearance (Magallón et al., 1999) have established the origin of Apocynaceae in the Early Eocene (ca. 53 million years ago (Ma)) or later (ca. 45 Ma; Magallón & Sanderson, 2001; Wikström et al., 2001). Nested within Apocynaceae, Asclepiadoideae have a later origin, having few known land routes available to explain their dispersals from the Old

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World into the New World. The aim of this study is to explore current distribution and phylogenetic relationships of the New World Asclepiadoideae in order to make inferences about their origin and diversification.

MATERIAL AND METHODS

We attempted to sample all species of New World Asclepiadoideae employed in molecular phylogenetic studies. The data matrix consisted of 216 sequences of *trnL* intron and *trnL-F* intergenic spacer (*trnL-F*), the most used markers at this taxonomic level in Asclepiadoideae. Most asclepiad sequences (175) were previously used in Rapini et al. (2003) and Liede-Schumann et al. (2005), but a few sequences were added (e.g., Liede & Täuber, 2002; Meve & Liede, 2004; Rapini et al., 2006) to improve sampling in particular regions of the tree. Gelseminaceae and Loganiaceae were collectively used as outgroups; samples from other subfamilies of Apocynaceae, namely Apocynoideae, Rauvolfioideae, Periplocoideae, and Secamonoideae were also included (Appendix I).

Bayesian analysis was carried out in MrBayes 3.1 (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003). The substitution model selected was GTR+G, estimated through hierarchical likelihood ratio tests (hLRT) in MrModeltest 2.2 (Nylander, 2004) as the one that better fits our data. We ran 1,000,000 generations, sampling a tree every 100 generations. The majority rule consensus was then built in PAUP* 4.0b10 (Swofford, 2001) using trees of the two runs (burn-in trees excluded) to generate the object tree. The topology obtained was then used for maximum likelihood branch-length optimization using PAUP* and the general model, and parameters previously estimated in MrModeltest. Molecular clock assumption was tested and rejected by likelihood ratio tests (LRT). Based on the branch-lengths, we then estimated absolute and relative rates for the tree through nonparametric rate smoothing (NPRS) using the software r8s (Sanderson, 1997). Based on a compromise between fossil and molecular lines of evidence (above), we converted relative to absolute ages calibrating the Apocynaceae crown group in the Paleocene/Eocene boundary (54 Ma). However, an alternative calibration in the Apocynaceae stem group at the same period was also considered.

RESULTS

The data matrix for the plastid *trnL-F* (available upon request from AR) included 1327 characters (146 characters of dubious alignment were excluded). The cold chain in the two independent runs reached

stabilization of likelihood values at about 80,000 generations. We discarded 10% of the trees (burn-in) in each run, summarizing the data based on the remaining 9001 trees of the two runs.

Previous phylogenetic studies (Rapini et al., 2003, 2006; Liede-Schumann et al., 2005) have already discussed topological relationships among these groups. Here, we restrict the results to the information present in the chronogram (Figs. 1–5). Differences between the two calibrations (crown and stem group) do not exceed 10 million years in most basal nodes of Asclepiadoideae, and the precision of estimates decreases with the distance from the calibration point. Therefore, these differences do not greatly affect overall biogeographical interpretations of New World Asclepiadoideae events, and the alternative calibration in the Apocynaceae stem group is omitted below.

With our calibration of the Apocynaceae crown group at 54 Ma, the Asclepiadoideae emerged at 40 Ma, the Asclepiadeae at 35 Ma, and the Marsdenieae and Ceropegieae at 30 Ma. The New World clade of *Marsdenia* would have appeared after 16 and radiated at 9.9 Ma (Fig. 1).

In Asclepiadeae, the Astephaninae arose at 33 Ma but became diverse only at 4.9 Ma. MOG and ACT clades (see introduction for definitions) diverged at 32 Ma. ACT diversified, giving rise to important groups (Tylophorinae, Asclepiadinae, and Cynanchinae) at around 27 Ma. The New World *Asclepias* diverged from African Asclepiadinae at 20 Ma. The South American group (including *A. curassavica* L.) arose between 16 and 7.5 Ma (Fig. 2). The New World *Cynanchum* (subg. *Mellichampia*) appeared at 24 Ma, diverging between North and South American species around 20 Ma (Fig. 3).

In the MOG clade, basal genera *Diplolepis* and *Pentacyphus*, as well as Orthosiinae and the MOG core group, appeared at 27 Ma. The Orthosiinae had events of diversification at 17 and 14 Ma, with a secondary diversification in *Orthosia* Decne. at 3.7 Ma. The MOG core group diversified at 24 Ma, having *Funastrum* E. Fourn. radiating at 16 Ma, *Tassadia* Decne. at 7 Ma, and the Gonolobinae at 15 Ma (Fig. 4). The Oxypetalinae became diverse at 15 Ma, with secondary events of diversification in *Philibertia* Kunth and *Oxypetalum* R. Br. at about 8 Ma (Fig. 5A). The Metastelmatinae became diverse only at 12 Ma, with secondary events of diversification in *Minaria* T. U. P. Konno & Rapini at 4.7 Ma and in the *Blepharodon* Decne.–*Hemipogon* Decne. clade at 2.6 Ma (Fig. 5B).

Absolute rates of diversification for clades in New World Asclepiadoideae ranged from 0.0407 speciation events per million years in *Pentacyphus* to 0.3245 in the sister group of *Blepharodon* s. str. Among the

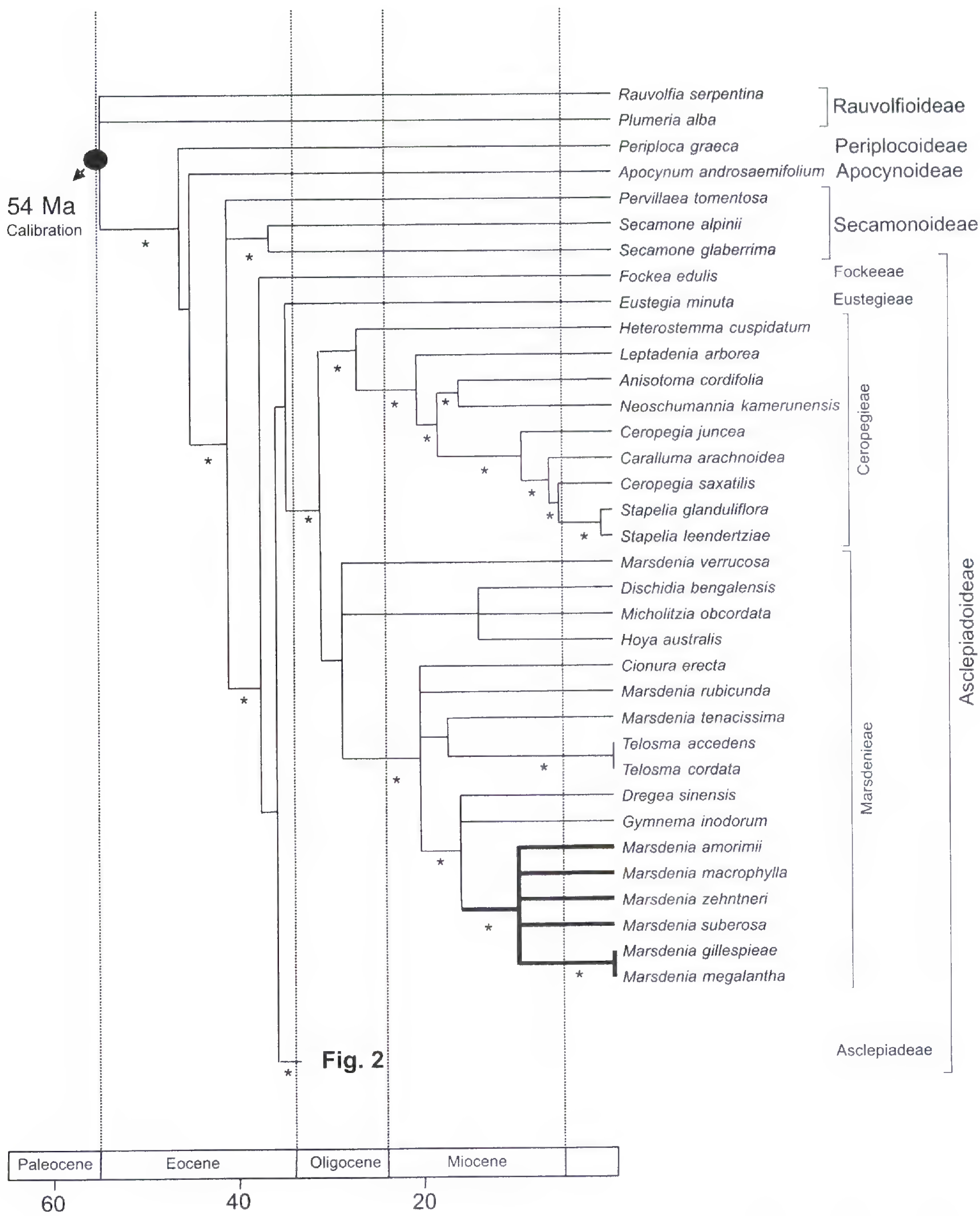


Figure 1. Lower portion of the Apocynaceae chronogram. New World clades are in bold lines. Asterisks (*) identify clades with posterior probability greater than 94%. Scale units are million years ago (Ma).

New World lineages of Asclepiadoideae, *Marsdenia* presented the highest rate of diversification (0.2655) and *Cynanchum* subg. *Mellichampia* the lowest (0.1306). *Asclepias* and the MOG group presented intermediary rates (0.2414 and 0.2075, respectively), the former similar to that in MOG core group (0.2416; Table 1).

DISCUSSION

Biogeographical studies have greatly changed in the past few years. Traditional cladistic biogeography (Nelson & Platnick, 1981) based on general area cladograms derived from topological congruencies is giving way to an integrative historical biogeography

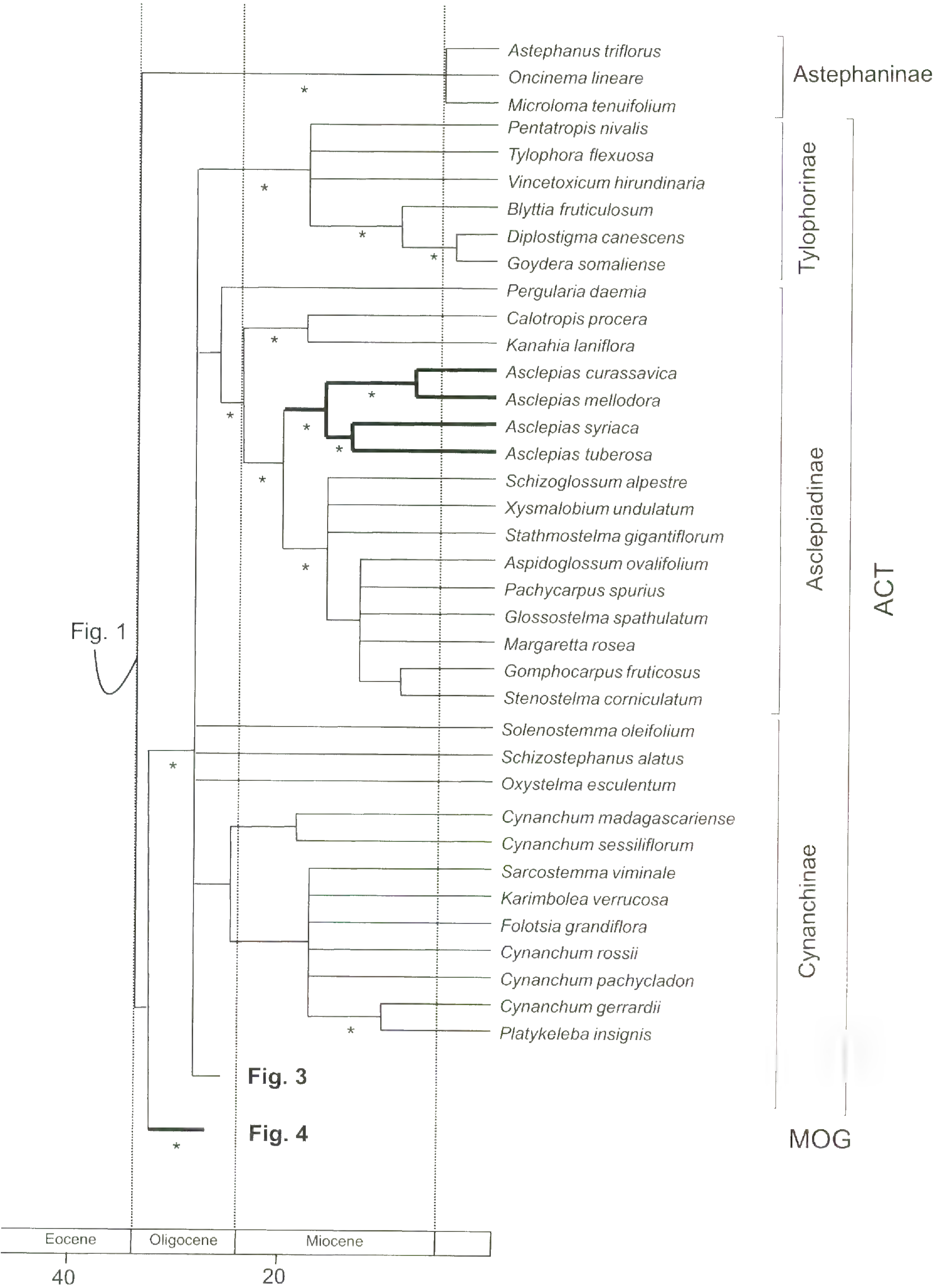


Figure 2 (continued from Fig. 1). Upper portion of the chronogram in Figure 1 (Asclepiadeae). New World clades are in bold lines. Asterisks (*) identify clades with posterior probability greater than 94%.

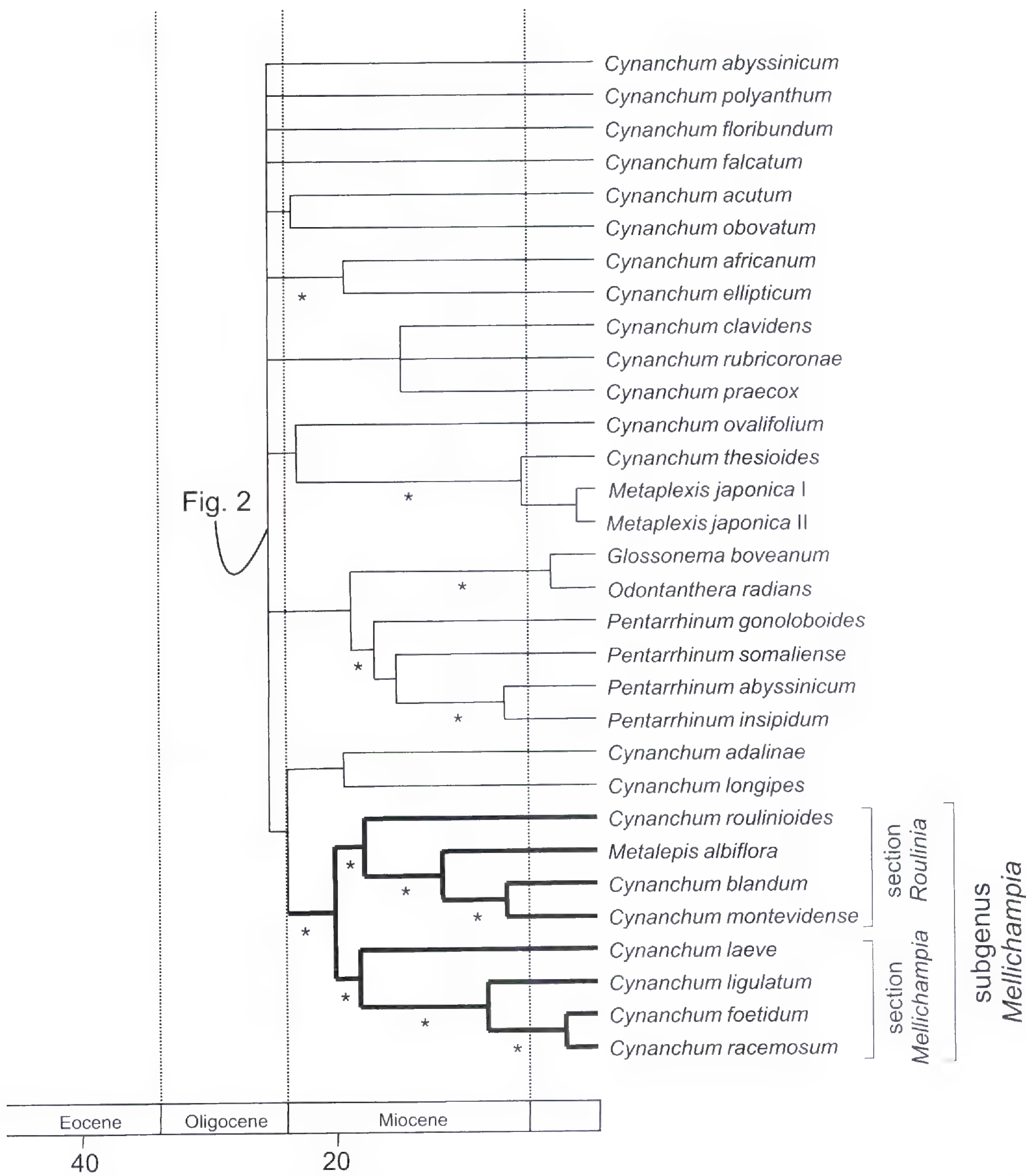


Figure 3 (continued from Fig. 2). Upper portion of the chronogram in Figure 2 (part of Cynanchinae). New World clades are in bold lines. Asterisks (*) identify clades with posterior probability greater than 94%.

(Donoghue & Moore, 2003). Molecular phylogenetic data allow estimates of clade ages, making the association of patterns of dispersal and diversification to climate and geological events more realistic, while also demonstrating the temporal complexity of organism distribution by exposing pseudocongruencies (Riddle, 2005, e.g., similar topologies with different time frames). New evidence on the evolution of plants has presented difficulties in explaining the distribution of some groups. Ages estimated for the

migration of several plants to the New World are not synchronic as would be expected in cases of single vicariant events, nor are they congruent with dates believed to allow intercontinental migration through land bridges (Pennington & Dick, 2004). These and many other examples have brought back long-distance dispersal as a feasible explanation in the scenario of biogeography (Queiroz, 2005).

Based on the data available and calibration assumed, the Asclepiadoideae originated at most in

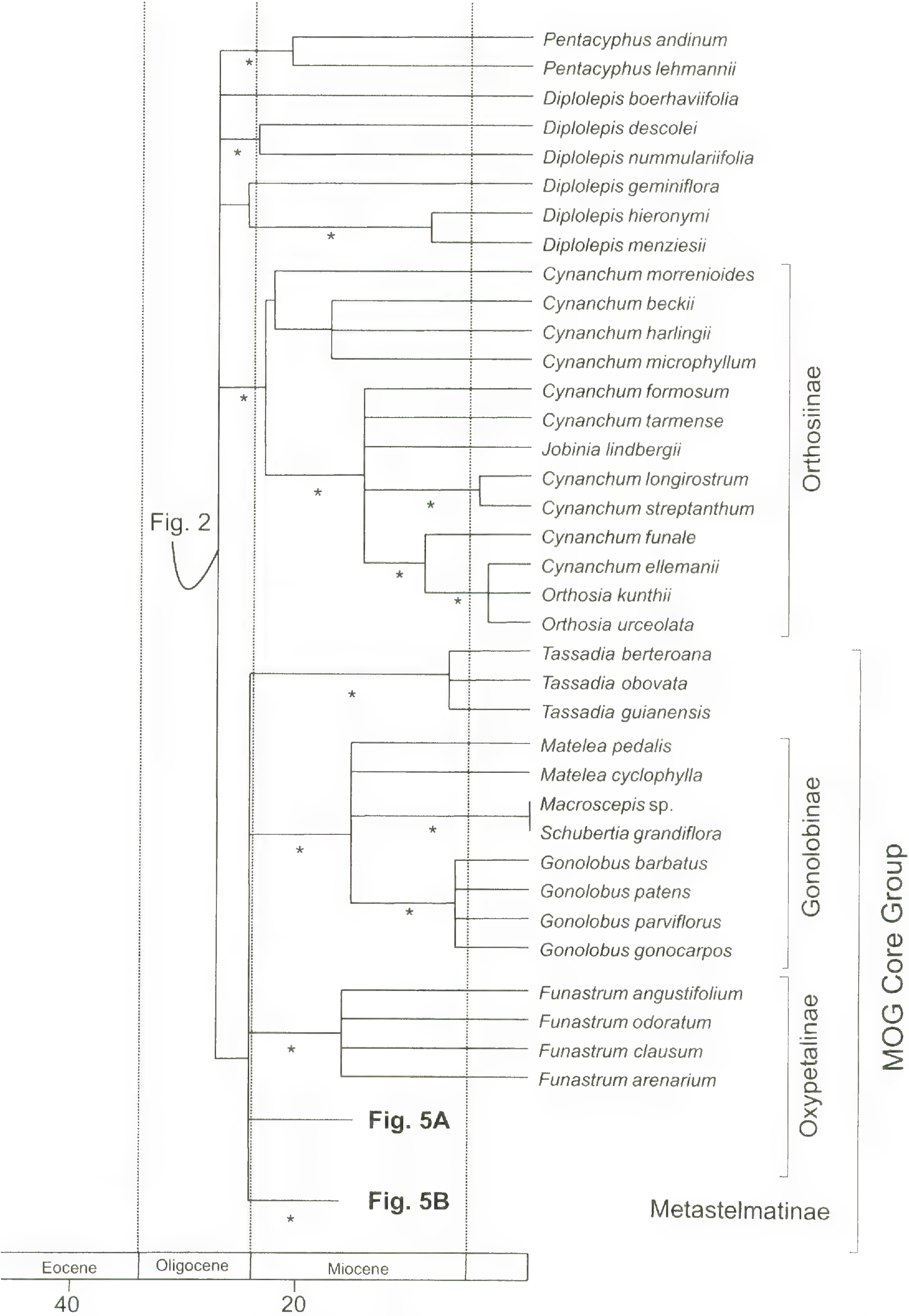


Figure 4 (continued from Fig. 2). Upper portion of the chronogram in Figure 2 (MOG). Asterisks (*) identify clades with posterior probability greater than 94%.

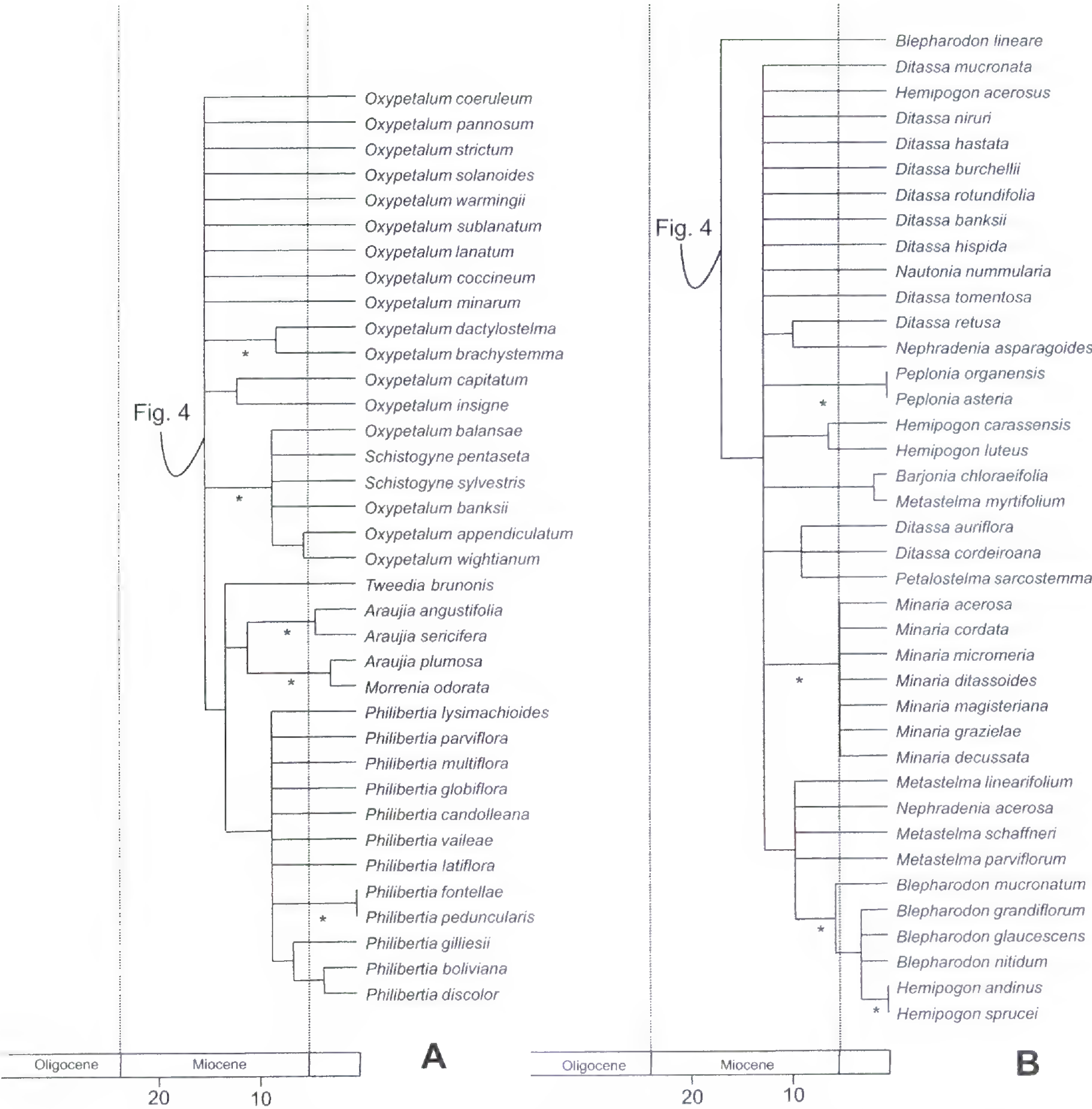


Figure 5 (continued from Fig. 4). Upper portion of the chronogram in Figure 4. —A. Oxypetalinae core group. —B. Metastelmatinae. Asterisks (*) identify clades with posterior probability greater than 94%.

the Late Eocene; fossil references of Asclepiadoideae in the Paleocene (e.g., LaMotte, 1952), therefore, must be treated with caution. Biogeographical events in the subfamily were not under the influence of Cretaceous continental drift that affected major floras before the Late Cretaceous (Raven & Axelrod, 1974a, b), and long-distance dispersals must be considered to explain intercontinental disjunctions between New and Old Worlds Asclepiadoideae. To determine the direction of dispersals in the discussion below, we usually assumed that if a derived clade A from an area X is nested in a grade composed of terminals from area Y, jump dispersal from Y to X is more likely. Directional asymmetry for long-distance dispersal, however, may make this assumption less simplistic (Cook & Crisp, 2005).

ORIGIN AND DIVERSIFICATION OF THE NEW
WORLD ASCLEPIADOIDEAE

The Asclepiadoideae colonized the New World at four different times, suggesting independent dispersals from the Old World rather than any kind of vicariant event. The clade with Metastelmatinae, Oxypetalinae, and Gonolobinae (MOG, see introduction) was the first to arrive, at 32 Ma (Fig. 2); three other invasions were more recent, with *Cynanchum* at around 24 Ma (Fig. 3), *Asclepias* 20 Ma (Fig. 2), and *Marsdenia* 16 Ma (Fig. 1). Between 32 and 16 Ma, South America was a continental island (Raven & Axelrod, 1974a, b). In contrast, North America was connected to eastern Asia through the Bering Strait, a route probably permeable for temperate taxa until

Table 1. Number of species, age, and rates of speciation for New World Asclepiadoideae clades.

Clade	Species no. (n) ¹	Age (t) ²	Rate of speciation ³
MOG	766	32	0.2075
<i>Pentacyphus</i>	3	27	0.0407
<i>Diplolepis</i>	6	27	0.0664
Orthosiinae	77	27	0.1609
MOG core group	680	27	0.2416
<i>Tassadia</i>	24	24	0.1324
Gonolobinae	280	24	0.2348
<i>Funastrum</i>	17	24	0.1010
Other Oxypetalinae	177	24	0.2157
<i>Blepharodon</i>	2	16	0.0433
Other Metastelmatinae	180	16	0.3245
<i>Asclepias</i>	125	20	0.2414
<i>Cynanchum</i> subg. <i>Mellichampia</i>	23	24	0.1306
<i>American Marsdenia</i>	70	16	0.2655

¹ estimates.
² million years; based on stem group.
³ speciation events per million years; birth-and-death model and extinction considered negligible: ln(n)/t.

the end of the Oligocene, but possibly later (Tiffney, 1985a).

MOG is a predominantly South American clade that comprises three quarters of New World Asclepiadoideae. It is characterized by a basal grade composed of the small South American genera *Pentacyphus* and *Diplolepis*, followed by the predominantly South American Orthosiinae (Liede-Schumann et al., 2005). This suggests that the first New World Asclepiadoideae arrived in South America. This colonization during the Oligocene must be explained by a transoceanic dispersal from Africa, the likely birthplace of the Asclepiadoideae. It is possible that the African Walvis Ridge and the South American Rio Grande Rise were above sea at this time, reducing the distance between the two continents (Renner, 2004), and long-distance dispersals between Africa and South America have been proposed to explain the origin of a substantial proportion of the Neotropical flora (Pennington & Dick, 2004).

The MOG core group arose at the end of Oligocene (Fig. 4). There is no consistent resolution for the relationship among the subtribes (Rapini et al., 2006), although the Metastelmatinae probably diverged first and the Oxypetalinae and Gonolobinae form a clade including *Tassadia* (Liede-Schumann et al., 2005).

The Metastelmatinae are well distributed along the Neotropics but reach higher diversity in the mountainous regions of the northern South America and central Brazil and in the Caribbean islands. This subtribe emerged in the Late Oligocene (24 Ma; Fig. 4) and radiated in the mid-Miocene (12 Ma; Fig. 5B). *Blepharodon* s. str., with two species restricted to central South America, was the first genus to diverge from the group, followed by a South

American grade composed of *Minaria* and *Barjonia* Decne.–*Nephradenia* Decne. clade (Liede-Schumann et al., 2005; Rapini et al., 2006). *Minaria* includes 19 species, most of them restricted to small areas of the Espinhaço mountain range in Minas Gerais, Brazil (Konno et al., 2006). The genus arose at 12 Ma but did not radiate until 4.7 Ma, in the Tertiary–Quaternary boundary (Fig. 5B), denoting a relatively recent diversification in Brazilian shields. The *Barjonia*–*Nephradenia* clade comprises around a dozen species dispersed in central South America. The rest of Mestastelmatinae are divided into a few genera, the largest ones being *Ditassa* R. Br. and *Metastelma* R. Br. *Ditassa* is more diverse eastward of the tropical Andes, except in the Amazonian region, and *Metastelma* is predominantly distributed in the Caribbean islands (Liede & Meve, 2004). Their circumscription is still open, as well as the position of the smaller genera, which depends on further resolution of relationships in Metastelmatinae core group. The subtribe is therefore composed of a South American grade, in which the Central American species nest. Most species inhabit disturbed and/or open vegetation, which may have favored wind dispersal from South America to the Caribbean islands and their secondary diversification there.

The Oxypetalinae are most diverse in central South America, with the number of species greatly decreasing northward. The disproportionate distribution of Oxypetalinae in the Neotropics suggests that a primary diversification of the subtribe occurred between 15–30 S, in central South America, during the mid-Miocene (Fig. 5A). *Funastrum* was the first genus to diverge in the evolution of the subtribe (Liede-Schumann et al., 2005; Rapini et al., 2006).

Arising in South America, *Funastrum* dispersed northward, becoming more diverse in Central and North America at 16 Ma (Fig. 4). Apart from *Funastrum*, the Oxypetalinae are divided into two main clades (Rapini et al., 2006), one predominantly in southeastern South America comprising *Oxypetalum* R. Br. (including *Schistogyne* Hook. & Arn.), and the other predominantly in southwestern South America comprising *Tweedia* Hook. & Arn., *Araujia* Brot.–*Morrenia* Lindl., and *Philibertia* Kunth. *Oxypetalum* is the largest genus in the subtribe, with most species occurring in northern Argentina and southern and southeastern Brazil, but *O. cordifolium* (Vent.) Schltr. can reach as far as Mexico and Cuba. Like *Funastrum*, *Oxypetalum* radiated at 16 Ma, having a second event of diversification at around 8 Ma, coinciding with *Philibertia* diversification (Fig. 5A).

The Gonolobinae are widespread in the Neotropics, presenting higher diversity from northern South America to Mexico. The circumscriptions of *Matelea* Aubl. and *Gonolobus* Michx., the two largest genera of Gonolobinae, are still open and the recognition of several genera in the subtribe depends on them. The subtribe emerged between the Oligocene and Miocene, presenting two episodes of diversification—an initial one at 15 Ma, and a second event in *Gonolobus* at 6.4 Ma (Fig. 4). From an initial diversification of the MOG core group in central South America, Gonolobinae would have dispersed west- and northward, radiating in northern South America and Central America, but not in the Caribbean islands, and ultimately reaching North America, where the subtribe is also well represented.

Tassadia is phylogenetically closer to Oxypetalinae and/or Gonolobinae than to Metastelmatinae (Liede-Schumann et al., 2005). The genus would have emerged during the initial diversification of the MOG core group but radiated only in the Late Miocene (Fig. 4). Most *Tassadia* species are concentrated in northern South America (Fontella-Pereira, 1977), with over half of them occurring in Venezuela. The most widespread species, *T. obovata*, reaches Santa Catarina in southern Brazil and Nicaragua to the North, and is the only species of *Tassadia* to cross the Isthmus of Panama into Central America.

The Cynanchinae are not yet well resolved in the ACT (Asclepiadinae, Cynanchinae, Tylophorinae) clade (Rapini et al., 2003), and *Cynanchum* (sensu Liede & Täuber, 2002), though not contradicted, was not detected with *trnL-F* (Rapini et al., 2003). The New World species, however, form a well-supported clade, the subgenus *Mellichampia* (Fig. 3; Liede & Kunze, 2002; Liede & Täuber, 2002; Rapini et al., 2003). This group is poorly diversified in the whole

Neotropics, and according to phylogenetic studies with molecular data (e.g., Liede & Kunze, 2002), it can be roughly divided into North (section *Mellichampia* Sundell) and South (section *Roulinia* Sundell) American sections. However, *C. racemosum* (Jacq.) Jacq. is widespread in Central America, reaching northern South America, and *C. monteridense* Spreng. is widespread in South America, reaching Panama. Derivation of the two species, *C. racemosum* in section *Mellichampia* and *C. monteridense* in section *Roulinia* (Fig. 3), suggests that the occurrence of these species in South and Central America, respectively, is the result of relatively recent biotic expansions. Unlike the other three New World Asclepiadoideae lineages, the subgenus presented a slow, gradual accumulation of species since its origin in the Late Oligocene.

The Asclepiadinae arose in the Oligocene, reaching the New World in the Miocene (Fig. 2). *Asclepias* is the only American genus of the subtribe. Different from MOG, it is a predominantly North American group that is able to survive in colder regions. The number of species decreases southward, almost disappearing in the tropics but becoming more diverse in subtropical South America. *Asclepias* is sister to the African Asclepiadinae and is probably characterized by a basal grade of North American species, in which the South American clade is nested (Rapini et al., 2003; Goyder et al., 2007, this issue). The Asclepiadinae probably arrived in the New World through North America, dispersing to Central and South America. The North Atlantic passageway between Africa and North America persisted only until the Eocene (Tiffney, 1985b), and the increasingly cooler temperatures during the Late Tertiary made the connection between eastern Asia and western North America questionable (Tiffney, 1985a). As in Asclepiadinae, however, many plant disjunctions between Asia and North America seem to be more recent than 30 Ma, suggesting that plants have a high capacity for dispersing over long distances and establishing founder populations and that they also have higher extinction rates when compared to animals (Donoghue & Smith, 2004; Pennington & Dick, 2004). In this context, the Asclepiadinae have been able to disperse from Asia to North America, the predominant direction for plants, at around 20 Ma, through the Bering Strait during one of the several warm intervals that took place between Early Oligocene and mid-Miocene (Graham, 1999). The assumed Asian sister group of *Asclepias*, however, is hypothesized as extinct.

Although the South American *Asclepias* form a small, morphologically uniform group easily recognized by their white flowers, phylogenetically, the

colored flower *A. curassavica* is probably closer to them than to the North American species. If the species is originally North American, *Asclepias* would have dispersed to South America at 7.5 Ma. At this time, the Panamanian Isthmus was not yet established but probably supported a step-stone dispersal between the two continents. Alternatively, if *A. curassavica* is native to South America, this dispersal would be pushed to between 16 and 7.5 Ma, with the explanation for the dispersal to South America through long-distance dispersal or, at best, a step-stone migration through available inter-island passages (Coney, 1982). After arriving in South America, *Asclepias* has either diversified on the southern continent or evenly colonized the continent during cooler periods, and it was subject to extinction in tropical areas when the climate became warmer.

The Marsdenieae presumably arose in the Oligocene, arriving in the New World during the mid-Miocene and radiating in the Late Miocene (Fig. 1). *Marsdenia* is the only genus of Marsdenieae in the New World, inhabiting a wide range of vegetations from moist Amazonian forest in northern South America to dry caatinga in northeastern Brazil. The origin of *Marsdenia* in the New World is unclear, particularly because the group is poorly sampled and relationships to the American clade are unresolved. It is unlikely that they arrived in the New World via North America during the Miocene because the Bering Strait is believed to have been closed for megathermal plants since the Eocene (Tiffney, 1985a). The most plausible explanation is that *Marsdenia* arrived in South America by long-distance dispersal and shared the common northward dispersal route of New World lianas (Gentry, 1982), from tropical South America to Mesoamerica, probably through the Isthmus of Panama.

PATTERNS OF DIVERSIFICATION IN THE NEW WORLD ASCLEPIADOIDEAE

In Asclepiadoideae, invasions of the New World occurred in different periods of the Tertiary, involving long-distance dispersals from the Old World. The current diversity of the MOC clade, the oldest and most diverse Neotropical lineage of Asclepiadoideae, is concentrated in particular clades of the core group with higher rates of diversification, reflecting successive radiations, mainly during the Late Oligocene and mid-Miocene (Figs. 4, 5). The Late Oligocene is marked by a relatively warm temperature followed by the short-term Miocene glaciation, and the mid-Miocene marks the climatic optimum, between 15 and 16 Ma (Zachos et al., 2001).

The pattern of diversification detected in the MOC core group differs from that observed for elements of

the Amazonian flora. Several species in *Funastrum*, *Oxypetalum*, and *Ditassa* are probably older than 10 Ma. On the other hand, evidence from phylogenetic studies in *Inga* Mill. (Richardson et al., 2001), a predominantly Amazonian species-rich genus of trees, shows speciation events concentrated in the past 10 Ma, with many species as young as 2 Ma or less. In some aspects, the pattern found in MOC diversification appears to be similar to that detected in Neotropical seasonally dry forest plants, whose lineages are also marked by multiple events of rapid speciation from the mid-Miocene to the Pliocene, resulting in a mosaic of ancient and recent species (Pennington et al., 2004).

The American *Cynanchum* were characterized by slow, gradual accumulation of species, allowing good resolution of relationships among them (Fig. 3). The relatively high rate of diversification of American *Marsdenia*, its recent dispersal to the Neotropics, and the unresolved relationship among species sampled here suggest that the group diversified by radiation. Based on the rate of diversification in *Asclepias*, similar to that of MOC core group, a diversification by radiations might also be assumed.

Somewhat synchronic radiations in MOC and ACT during the Late Oligocene, as well as among subtribes of MOC core group during the mid- and Late Miocene, suggest an important influence of global environmental factors in the Asclepiadoideae diversification. Intrinsic factors, however, have also played an essential role in their diversification, and they are probably the main reason why some lineages (e.g., *Pentacyphus*, *Diplolepis*, and *Blepharodon* s. str. in MOC, and *Cynanchum* subg. *Mellichampia* in Cynanchinae) have been subject to a remarkably low rate of diversification (unless extinction was extensive in these groups).

Together, these data suggest that there is not a single key element responsible for the diversification of Asclepiadoideae in the New World. Neither intrinsic innovations nor global extrinsic factors alone can explain this diversity. The imbalance of diversification in the clades of MOC seems to follow the general pattern observed in angiosperms as a whole, a complex process driven by interactive effects of biological traits and environmental factors (Davies et al., 2004). Apparently, most diversity, particularly in the MOC core clade, was the result of pulses of radiation allowed by intrinsic properties of lineages but motivated by environmental factors.

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Appendix 1. List of taxa and GenBank accession numbers. Asclepiad sequences were previously published in Rapini et al. (2003) and Liede-Schuman et al. (2005), as well as Liede and Tauber (2002), Meve and Liede (2004), and Rapini et al. (2006); classification and organization follows Endress and Bruyns (2000), Rapini et al. (2003), and Liede-Schumann et al. (2005).

Taxa	Intron <i>trnL</i>	Intergenic spacer <i>trnL-F</i>
LOGANIACEAE		
<i>Strychnos tomentosa</i> Benth.	AF214301	AF214147
GELSEMINACEAE		
<i>Gelsemium sempervirens</i> (L.) J. St.-Hil.	AF102428	AF159696
APOCYNACEAE		
Apocynoidae		
<i>Apocynum androsaemifolium</i> L.	AF214308	AF214154
Asclepiadoideae, Asclepiadeae		
Asclepiadeae, Astephaninae		
<i>Astephanus triflorus</i> R. Br	AJ410188	AJ410189
<i>Microloma tenuifolium</i> K. Schum.	AJ410221	AJ410222
<i>Oncinema lineare</i> (L. f.) Bullock	AJ410230	AJ410231
Asclepiadeae, ACT (Asclepiadinae, Cynanchinae, Tylophorinae)		
Asclepiadeae, Asclepiadinae		
<i>Asclepias curassavica</i> L.	AY163664	AY163664
<i>Asclepias mellodora</i> A. St.-Hil.	AY163665	AY163665
<i>Asclepias syriaca</i> L.	AF214311	AJ410180
<i>Asclepias tuberosa</i> L.	AF214312	AF214158
<i>Aspidoglossum oralifolium</i> (Schltr.) Kupicha	AY163666	AY163666
<i>Calotropis procera</i> (Aiton) W. T. Aiton	AF214324	AF214170
<i>Glossostelma spathulatum</i> (K. Schum.) Bullock	AY163686	AY163686
<i>Gomphocarpus fruticosus</i> (L.) W. T. Aiton	AY163687	AY163687
<i>Kanahia laniflora</i> (Forssk.) R. Br.	AY163695	AY163695
<i>Margaretta rosea</i> Oliv.	AY163696	AY163696
<i>Pachycarpus spurius</i> (N. E. Br.) Bullock	AY163716	AY163716
<i>Pergularia daemia</i> (Forssk.) Chiov.	AJ290892	AJ290893
<i>Schizoglossum alpestre</i> K. Schum.	AY163718	AY163718
<i>Stathmostelma gigantiflorum</i> K. Schum.	AY163721	AY163721
<i>Stenostelma corniculatum</i> (E. Mey.) Bullock	AY163722	AY163722
<i>Xysmalobium undulatum</i> (L.) W. T. Aiton	AY163725	AY163725
Asclepiadeae, Cynanchinae		
<i>Cynanchum abyssinicum</i> Decne.	AJ428580	AJ428581
<i>Cynanchum acutum</i> L.	AJ428583	AJ428584
<i>Cynanchum adalinae</i> K. Schum.	AJ428586	AJ428587
<i>Cynanchum africanum</i> Hoffmanns.	AJ428589	AJ428590
<i>Cynanchum blandum</i> (Decne.) Sundell	AJ428604	AJ428605
<i>Cynanchum clavidens</i> N. E. Br.	AJ428610	AJ428611
<i>Cynanchum ellipticum</i> (Harv.) R. A. Dyer.	AJ290846	AJ290845
<i>Cynanchum falcatum</i> Hutch. & E. A. Bruce	AJ428631	AJ428632
<i>Cynanchum floribundum</i> R. Br.	AJ428634	AJ428635
<i>Cynanchum foetidum</i> (Cav.) Kunth	AJ428637	AJ428638
<i>Cynanchum gerrardii</i> (Harv.) Liede	AJ428646	AJ428647
<i>Cynanchum laeve</i> (Michx.) Pers.	AJ428652	AJ428653
<i>Cynanchum ligulatum</i> (Benth.) Woodson	AJ428658	AJ428659
<i>Cynanchum longipes</i> N. E. Br.	AJ428664	AJ428665
<i>Cynanchum madagascariense</i> K. Schum.	AJ428667	AJ428668
<i>Cynanchum monteridense</i> Spreng.	AJ290849	AJ290850
<i>Cynanchum obovatum</i> (Decne.) Choux.	AJ428802	AJ428803

Appendix 1. Continued.		
Taxa	Intron <i>trnL</i>	Intergenic spacer <i>trnL-F</i>
<i>Cynanchum ovalifolium</i> Wight	AJ428697	AJ428698
<i>Cynanchum pachycladon</i> Choux	AJ428700	AJ428701
<i>Cynanchum polyanthum</i> (K. Schum.) K. Schum.	AJ428712	AJ428713
<i>Cynanchum praecox</i> Schltr. ex S. Moore	AJ428715	AJ428716
<i>Cynanchum racemosum</i> (Jacq.) Jacq.	AJ428721	AJ428722
<i>Cynanchum rossii</i> Rauh	AJ428730	AJ428731
<i>Cynanchum roulinioides</i> (E. Fourn.) Rapini	AJ428733	AJ428734
<i>Cynanchum rubricorona</i> Liede	AJ428736	AJ428737
<i>Cynanchum sessiliflorum</i> (Decne.) Liede	AJ428742	AJ428743
<i>Cynanchum thesioides</i> (Freyn) K. Schum.	AJ428748	AJ428749
<i>Folotsia grandiflora</i> (Jum. & H. Perrier) Jum. & H. Perrier	AJ290855	AJ290856
<i>Glossonema boveanum</i> (Decne.) Decne.	AY163684	AY163685
<i>Karimbolea verrucosa</i> Desc.	AJ290880	AJ290879
<i>Metalepis albiflora</i> Urb.	AJ428775	AJ428776
<i>Metaplexis japonica</i> Makino (I)	AJ428811	AJ428812
<i>Metaplexis japonica</i> Makino (II, wrongly assigned to <i>Cynanchum auriculatum</i> Buch.-Ham. ex Wight in previous studies)	AJ410197	AJ410198
<i>Odontanthera radians</i> (Forssk.) D. V. Field	AJ428814	AJ428815
<i>Pentarrhinum abyssinicum</i> Decne.	AJ428817	AJ428818
<i>Pentarrhinum gonoloboides</i> (Schltr.) Liede	AJ428820	AJ428821
<i>Pentarrhinum insipidum</i> E. Mey.	AJ410233	AJ410234
<i>Pentarrhinum somaliense</i> (N. E. Br.) Liede	AJ428823	AJ428824
<i>Platykeleba insignis</i> N. E. Br.	AJ290907	AJ290906
<i>Sarcostemma viminale</i> (L.) R. Br.	AJ290913	AJ290912
<i>Schizostephanus alatus</i> Hochst. ex K. Schum.	AJ410248	AJ410249
Asclepiadeae, Tylophorinae		
<i>Biondia henryi</i> (Warb. ex Schltr. & Diels) Tsiang & P. T. Li	AJ410191	AJ410192
<i>Blyttia fruticulosa</i> (Decne.) D. V. Field	AJ410194	AJ410195
<i>Diplostigma canescens</i> K. Schum.	AJ410200	AJ410201
<i>Goydera somaliensis</i> Liede	AJ410209	AJ410210
<i>Pentatropis nivalis</i> (J. F. Gmel.) D. V. Field & J. R. I. Wood	AJ410239	AJ410240
<i>Tylophora flexuosa</i> R. Br.	AJ290916	AJ290917
<i>Vincetoxicum hirundinaria</i> Medik.	AJ410275	AJ410276
Unplaced Genera		
<i>Oxystelma esculentum</i> (L. f.) Sm.	AJ290885	AJ290887
<i>Solenostemma oleifolium</i> (Nect.) Bullock & E. A. Bruce ex Bullock	AJ428832	AJ428833
Asclepiadeae, MOG (Metastelmatinae, Oxypetalinae, and Gonolobinae, plus Orthosiinae)		
Basal Grade		
<i>Diplolepis boerhaviifolia</i> (Hook. & Arn.) Liede & Rapini	AJ428607	AJ428608
<i>Diplolepis descolei</i> (T. Mey.) Liede & Rapini	AJ699304	AJ699302
<i>Diplolepis geminiflora</i> (Decne.) Liede & Rapini	AJ410182	AJ410183
<i>Diplolepis hieronymi</i> (Lorentz) Liede & Rapini	AJ410212	AJ410213
<i>Diplolepis menziesii</i> Schult.	AJ699273	AJ699275
<i>Diplolepis nummulariifolia</i> (Hook. & Arn.) Liede & Rapini	AJ290852	AJ290851
<i>Pentacyphus andinus</i> (Ball.) Liede	AJ492150	AJ492151
<i>Pentacyphus lehmannii</i> (Schltr.) Liede	AJ290889	AJ290888
Asclepiadeae, Gonolobinae		
<i>Gonolobus barbatus</i> Kunth	AJ704261	AJ704263
<i>Gonolobus gonocarpos</i> (Walter) L. M. Perry	AJ704277	AJ704276
<i>Gonolobus parviflorus</i> Decne.	AY163689	AY163689
<i>Gonolobus rostratus</i> (Vahl) Schult.	AF214362	AF214208
<i>Macroscelis</i> Kunth, sp. indet.	AJ704268	AJ704267
<i>Matelea cyclophylla</i> (Standl.) Woodson	AJ704269	AJ704272
<i>Matelea pedalis</i> (E. Fourn.) Fontella & E. A. Schwarz	AY163699	AY163699
<i>Schubertia grandiflora</i> Mart.	AJ428826	AJ428827
Asclepiadeae, Metastelmatinae		
<i>Barjonia chloraeifolia</i> Decne.	AY163667	AY163667

Appendix 1. Continued.		
Taxa	Intron <i>trnL</i>	Intergenic spacer <i>trnL-F</i>
<i>Blepharodon glaucescens</i> (Decne.) Fontella	AJ699289	AJ699291
<i>Blepharodon grandiflorum</i> Benth.	AJ290837	AJ290838
<i>Blepharodon lineare</i> (Decne.) Decne.	AY163668	AY163668
<i>Blepharodon mucronatum</i> Decne.	AJ290840	AJ290839
<i>Blepharodon nitidum</i> (Vell.) J. F. Macbr.	AY163669	AY163669
<i>Ditassa auriflora</i> Rapini	AJ704471	AJ704470
<i>Ditassa banksii</i> R. Br. ex Schult.	AY163674	AY163674
<i>Ditassa burchellii</i> Hook. & Arn.	AJ699296	AJ699295
<i>Ditassa cordeiroana</i> Fontella	AY163675	AY163676
<i>Ditassa hastata</i> Decne.	AJ704221	AJ704223
<i>Ditassa hispida</i> (Vell.) Fontella	AJ704478	AJ704480
<i>Ditassa mucronata</i> Mart.	AJ704259	AJ704278
<i>Ditassa niruri</i> Decne.	AJ428751	AJ428752
<i>Ditassa retusa</i> Mart.	AJ704283	AJ704282
<i>Ditassa rotundifolia</i> (Decne.) Baill. ex K. Schum.	AJ704284	AJ704286
<i>Ditassa subtrivialis</i> Griseb.	AJ428755	AJ428756
<i>Ditassa tomentosa</i> (Decne.) Fontella	AJ704484	AJ704486
<i>Hemipogon acerosus</i> Decne.	AJ704291	AJ704290
<i>Hemipogon andinum</i> Rusby	AJ704292	AJ704294
<i>Hemipogon luteus</i> E. Fourn.	AY163693	AY163693
<i>Hemipogon sprucei</i> E. Fourn.	AJ704299	AJ704298
<i>Metastelma linearifolium</i> A. Rich.	AJ428808	AJ428809
<i>Metastelma myrtifolium</i> Decne.	AJ704494	AJ704493
<i>Metastelma</i> sp. indet., aff. <i>parriflorum</i> R. Br.	AJ428778	AJ428779
<i>Metastelma schaffneri</i> A. Gray	AJ410215	AJ410216
<i>Minaria acerosa</i> (Mart.) T. U. P. Konno & Rapini	AJ699288	AJ699287
<i>Minaria cordata</i> (Turcz.) T. U. P. Konno & Rapini	AJ699297	AJ699299
<i>Minaria decussata</i> (Mart.) T. U. P. Konno & Rapini	AJ704220	AJ704219
<i>Minaria ditassoides</i> (Silveira) T. U. P. Konno & Rapini	AY163678	AY163678
<i>Minaria grazielae</i> (Fontella & Marquete) T. U. P. Konno & Rapini	AJ410203	AJ410204
<i>Minaria magisteriana</i> (Rapini) T. U. P. Konno & Rapini	AY163681	AY163681
<i>Minaria micromeria</i> (Decne.) T. U. P. Konno & Rapini	AJ704248	AJ704237
<i>Nautonia nummularia</i> Decne.	AJ410227	AJ410228
<i>Nephradenia acerosa</i> Decne.	AY163704	AY163705
<i>Nephradenia asparagoides</i> (Decn.) E. Fourn.	AY163706	AY163707
<i>Peplonia asteria</i> (Vell.) Fontella & E. A. Schwarz	AJ704300	AJ704302
<i>Peplonia organensis</i> (E. Fourn.) Fontella & Rapini	AY163688	AY163688
<i>Petalostelma sarcostemma</i> (Lillo) Liede & Meve	AJ428787	AJ428788
Asclepiadeae, Orthosiinae		
<i>Cynanchum beckii</i> Morillo	AJ704307	AJ704306
<i>Cynanchum ellemannii</i> Morillo	AJ428781	AJ428782
<i>Cynanchum formosum</i> N. E. Br.	AJ428640	AJ428641
<i>Cynanchum funale</i> Poir.	AY163703	AY163703
<i>Cynanchum harlingii</i> Morillo	AJ704308	AJ704310
<i>Cynanchum longirostrum</i> (K. Schum.) W. D. Stevens	AJ704315	AJ704314
<i>Cynanchum microphyllum</i> Kunth	AJ428682	AJ428683
<i>Cynanchum morrenioides</i> Goyder	AJ428685	AJ428686
<i>Cynanchum streptanthum</i> Malme	AJ704316	AJ704318
<i>Cynanchum tarmense</i> Schltr.	AJ428745	AJ428746
<i>Jobinia lindbergii</i> E. Fourn.	AY163694	AY163694
<i>Orthosia kunthii</i> Decne.	AJ428784	AJ428785
<i>Orthosia urceolata</i> E. Fourn.	AJ704323	AJ704325
Asclepiadeae, Oxypetalinae		
<i>Araujia angustifolia</i> Steud.	AJ704330	AJ704332
<i>Araujia plumosa</i> Schltr.	AJ704337	AJ704336
<i>Araujia sericifera</i> Brot.	AJ428793	AJ428794
<i>Funastrum angustifolium</i> (Pers.) Liede & Meve	AJ428760	AJ428761
<i>Funastrum arenarium</i> (Decne. ex Benth.) Liede	AJ290858	AJ290857

Appendix 1. Continued.		
Taxa	Intron <i>trnL</i>	Intergenic spacer <i>trnL-F</i>
<i>Funastrum clausum</i> (Jacq.) Schltr.	AJ290861	AJ290862
<i>Funastrum odoratum</i> Schltr.	AJ290870	AJ290871
<i>Morrenia odorata</i> (Hook. & Arn.) Lindl.	AJ704345	AJ704344
<i>Oxypetalum appendiculatum</i> Mart.	AY163709	AY163709
<i>Oxypetalum balansae</i> Malme	AJ704346	AJ704348
<i>Oxypetalum banksii</i> R. Br. ex Schult.	AY163710	AY163710
<i>Oxypetalum brachystemma</i> Malme	AJ704353	AJ704352
<i>Oxypetalum capitatum</i> Mart.	AY163711	AY163711
<i>Oxypetalum coccineum</i> Griseb.	AJ704329	AJ704326
<i>Oxypetalum coeruleum</i> (D. Don ex Sweet) Decne.	AJ704354	AJ704356
<i>Oxypetalum dactylostelma</i> Goyder	AJ704338	AJ704339
<i>Oxypetalum insigne</i> (Decne.) Malme	AY163712	AY163712
<i>Oxypetalum lanatum</i> Decne.	AJ704507	AJ704508
<i>Oxypetalum minarum</i> E. Fourn.	AY163713	AY163713
<i>Oxypetalum pannosum</i> Decne.	AJ704513	AJ704514
<i>Oxypetalum solanoides</i> Hook. & Arn.	AJ704361	AJ704360
<i>Oxypetalum strictum</i> Mart.	AY163714	AY163714
<i>Oxypetalum sublanatum</i> Malme	AY163715	AY163715
<i>Oxypetalum warmingii</i> (E. Fourn.) Fontella & Marquete	AJ704519	AJ704520
<i>Oxypetalum wightianum</i> Hook. & Arn.	AJ704524	AJ704523
<i>Philibertia boliviana</i> (Baill.) Goyder	AJ704233	AJ704232
<i>Philibertia candolleana</i> (Hook. & Arn.) Goyder	AJ410176	AJ410177
<i>Philibertia discolor</i> (Schltr.) Goyder	AY163700	AY163700
<i>Philibertia fontellae</i> Goyder	AJ492153	AJ492154
<i>Philibertia gilliesii</i> Hook. & Arn.	AJ290895	AJ290894
<i>Philibertia globiflora</i> Goyder	AJ704234	AJ704236
<i>Philibertia latiflora</i> (Griseb.) Goyder	AJ704241	AJ704242
<i>Philibertia lysimachioides</i> (Wedd.) T. Mey.	AJ290901	AJ290900
<i>Philibertia multiflora</i> (T. Mey.) Goyder	AJ704243	AJ704245
<i>Philibertia parviflora</i> (Malme) Goyder	AJ410224	AJ410225
<i>Philibertia peduncularis</i> (Benth.) Goyder	AJ704251	AJ704250
<i>Philibertia vaileae</i> (Rusby) Liede	AJ290904	AJ290905
<i>Schistogyne pentaseta</i> Rusby	AJ704252	AJ704254
<i>Schistogyne sylvestris</i> Hook. & Arn.	AJ410245	AJ410246
<i>Tweedia brunonis</i> Hook. & Arn.	AJ704260	AJ704258
Asclepiadoideae, MOG Unplaced Genus		
<i>Tassadia berteriana</i> (Spreng.) W. D. Stevens	AJ428790	AJ428791
<i>Tassadia guianensis</i> Decne.	AJ699280	AJ699279
<i>Tassadia obovata</i> Decne.	AJ699281	AJ699283
Asclepiadoideae, Ceropegieae		
<i>Anisotoma cordifolia</i> Fenzl	AJ410017	AJ410018
<i>Caralluma arachnoidea</i> (P. R. O. Bally) M. G. Gilbert	AJ410038	AJ410039
<i>Ceropegia juncea</i> Roxb.	AJ428799	AJ428800
<i>Ceropegia saxatilis</i> Jum. & H. Perrier	AJ410041	AJ410042
<i>Heterostemma cuspidatum</i> Decne.	AJ574829	AJ574828
<i>Leptadenia arborea</i> (Forssk.) Schweinf.	AJ574833	AJ574834
<i>Stapelia glanduliflora</i> Mass.	AJ402128	AJ402151
<i>Stapelia leendertziae</i> N. E. Br.	AF214424	AF214270
Asclepiadoideae, Eustegieae		
<i>Eustegia minuta</i> (L. f.) N. E. Br.	AJ410206	AJ410207
Asclepiadoideae, Fockeeae		
<i>Fockea edulis</i> K. Schum.	AF214353	AF214199
Asclepiadoideae, Marsdenieae		
<i>Cionura erecta</i> Griseb.	AJ410173	AJ410174
<i>Dischidia bengalensis</i> Colebr.	AF214343	AF214189
<i>Gymnema inodorum</i> (Lour.) Decne.	AJ431750	AJ431751
<i>Hoya australis</i> R. Br. ex J. Traill	AF214367	AF214213

Appendix 1. Continued.			
Taxa		Intron <i>trnL</i>	Intergenic spacer <i>trnL-F</i>
<i>Marsdenia amorimii</i> Morillo		AF214377	AF214223
<i>Marsdenia gillespieae</i> Morillo		AJ431756	AJ431757
<i>Marsdenia macrophylla</i> (Humb. & Bonpl. ex Schult.) E. Fourn.		AJ574821	AJ574822
<i>Marsdenia megalantha</i> Goyder & Morillo		AJ574836	AJ574835
<i>Marsdenia rubicunda</i> N. E. Br.		AJ574839	AJ574840
<i>Marsdenia suberosa</i> (E. Fourn.) Malme		AY163697	AY163697
<i>Marsdenia tenacissima</i> (Roxb.) Moon		AJ431759	AJ431760
<i>Marsdenia verrucosa</i> Decne.		AJ431762	AJ431763
<i>Marsdenia zehntneri</i> Fontella		AY163698	AY163698
<i>Micholitzia obcordata</i> N. E. Br.		AF214381	AF214227
<i>Neoschumannia kamerunensis</i> Schltr.		AJ410053	AJ410054
<i>Telosma accedens</i> (Blume) Backer		AJ431783	AJ431784
<i>Telosma cordata</i> Merr.		AF214280	AF102493
Periplocoideae			
<i>Periploca graeca</i> L.		AF102468	AF214244
Rauvolfioideae			
<i>Plumeria alba</i> L.		AF214408	AF214254
<i>Rauwolfia serpentina</i> (L.) Benth. ex Kurz		AF214415	AF214261
Secamonoideae			
<i>Pervillaea tomentosa</i> Decne.		AJ431768	AJ431769
<i>Secamone alpinii</i> Schult.		AJ428829	AJ428830
<i>Secamone glaberrima</i> K. Schum.		AF214420	AF214266